

# Universal Scaling in the Branching of the Tree of Life

E. Alejandro Herrada<sup>1</sup>, Claudio J. Tessone<sup>1,2</sup>, Konstantin Klemm<sup>3</sup>, Víctor M. Eguíluz<sup>1\*</sup>, Emilio Hernández-García<sup>1</sup>, Carlos M. Duarte<sup>4</sup>

**1** IFISC, Instituto de Física Interdisciplinar y Sistemas Complejos (CSIC-UIB), Palma de Mallorca, Spain, **2** ETH Zürich, Zürich, Switzerland, **3** Bioinformatics Group, Department of Computer Science, University of Leipzig, Leipzig, Germany, **4** IMEDEA, Instituto Mediterráneo de Estudios Avanzados (CSIC-UIB), Esporles, Spain

## Abstract

Understanding the patterns and processes of diversification of life in the planet is a key challenge of science. The Tree of Life represents such diversification processes through the evolutionary relationships among the different taxa, and can be extended down to intra-specific relationships. Here we examine the topological properties of a large set of interspecific and intraspecific phylogenies and show that the branching patterns follow allometric rules conserved across the different levels in the Tree of Life, all significantly departing from those expected from the standard null models. The finding of non-random universal patterns of phylogenetic differentiation suggests that similar evolutionary forces drive diversification across the broad range of scales, from macro-evolutionary to micro-evolutionary processes, shaping the diversity of life on the planet.

**Citation:** Herrada EA, Tessone CJ, Klemm K, Eguíluz VM, Hernández-García E, et al. (2008) Universal Scaling in the Branching of the Tree of Life. PLoS ONE 3(7): e2757. doi:10.1371/journal.pone.0002757

**Editor:** Enrico Scalas, University of East Piedmont, Italy

**Received:** April 9, 2008; **Accepted:** June 23, 2008; **Published:** July 23, 2008

**Copyright:** © 2008 Herrada et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Funding:** We acknowledge financial support from MEC (Spain) and FEDER, project FISICOS, from CSIC (Spain) project PIE 2007501016, from SBF (Switzerland) through project C05.0148 (Physics of Risk), and from the European Commission through the NEST-Complexity project EDEN. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors have declared that no competing interests exist.

\* E-mail: victor@ifisc.uib-csic.es

## Introduction

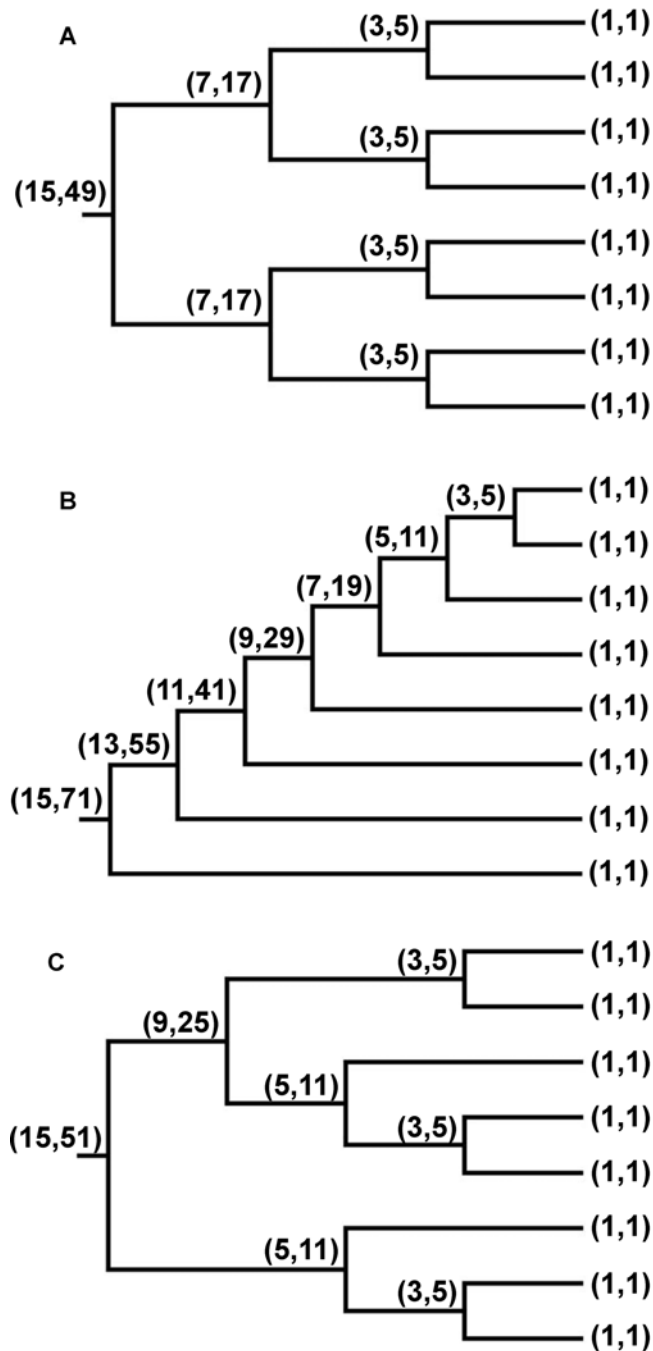
The Tree of Life is a synoptic depiction of the pathways of evolutionary differentiation between Earth life forms [1], and contains valuable clues on the key issue of understanding the diversification of life in the planet [2]. The branching pattern of the Tree of Life, which is being captured at increasing resolution by the advent of molecular tools [3], can be examined to investigate fundamental questions, such as whether it follows universal rules, and at what extent random differentiation mechanisms explain the shape of phylogenetic trees. The examination of the structure of the Tree of Life can also help to infer whether evolution acts at intraspecific scales in a way different from the action of evolution at the interspecific scale. Here we address these fundamental questions on the basis of a comprehensive comparative analysis of phylogenetic trees representing different fractions and domains of the Tree of Life, from interspecific to intraspecific scales. We draw from previous analyses of the geometry of the Tree of Life [4], the characterization of other branching systems [5,6], and using tools derived from modern network theory [7–10] to examine the scaling of the branching in the Tree of Life [11,12]. Our analysis is based on a thorough data set of more than 5000 interspecific phylogenies and a sample of 67 intraspecific phylogenies (see Text S1), thereby testing the universality of the results derived across scales.

A phylogenetic tree is a set of nodes, each node representing a diversification event, connected by branches (links). For each node  $i$ , a subtree  $S_i$  is made up of a root at node  $i$  and all the descendant nodes stemming from this root. The subtree size  $A_i$  gives the number of subtaxa that diversify from node  $i$  (including itself). Beyond this measure of the diversity degree, the characterization of how the diversity is arranged through the phylogenies can be achieved through the cumulative branch size,  $C_i$ , a measure of the

subtree shape. It is defined [13] as the sum of the branch sizes associated to all the nodes in the subtree  $S_i$ ,  $C_i = \sum A_j$ . For the same tree size, and restricting to binary branching events, the smallest value of the cumulative branch size is obtained for a completely symmetric, balanced tree, whereas the most asymmetric, the pectinate or comb-like tree in which all branches split successively from a single one, yields the largest  $C_i$  value [13]. To be clearer, we show in Figure 1 the analysis of  $A_i$  and  $C_i$  for a completely balanced tree (Figure 1A) and for a completely imbalanced tree (Figure 1B). A portion of a real phylogenetic tree is also shown (Figure 1C). How the shape of the tree (i.e., the distribution of the biological diversification) does change with tree size (i.e., with the number of taxa it contains) is given by the scaling of the subtree shape  $C$  vs. the subtree size  $A$ , as described by the allometric scaling relation  $C \sim A^\eta$ . We quantitatively characterize the shape of each tree in our data set by calculating the functions  $F(A)$  and  $F(C)$ , which are the complementary cumulative distribution functions (CCDF) of  $A_i$  and  $C_i$  values in the tree, respectively, and the value of the allometric scaling exponent,  $\eta$ . We compare the results derived from the analyses of inter- and intra-specific phylogenetic trees among them, to test for the preservation of branching patterns across evolutionary scales, and against those derived from the analyses of randomly-generated trees to test whether the allometric scaling derived can be modeled using simple, random branching rules.

## Results

The branch-size CCDF displays power-law tails of the form  $F(A) \sim A^{1-\tau_A}$  for large branch size  $A$  (Figure 2A). The power-law exponents  $\tau_A$  are remarkably similar for the data sets analyzed:  $\tau_A = 1.76 \pm 0.03$ , and  $1.74 \pm 0.02$  for intra- and interspecific phylog-



**Figure 1. Branch size and cumulative branch size examples.** The values of the branch size ( $A$ ) and of the cumulative branch size ( $C$ ) are shown (in brackets, as  $(A,C)$ ) at each node of three small example trees. A: a completely balanced tree of 15 nodes; B: a completely imbalanced tree of 15 nodes of a real phylogenetic tree, the intraspecific *Vibrio vulnificus* phylogeny presented in full in Fig. S2A. Note that the value of  $C$  at the root is maximum for the fully imbalanced tree, and minimum for the balanced one.  
doi:10.1371/journal.pone.0002757.g001

enies, respectively. Similarly, the cumulative-branch-size CCDF also displays a power-law tail of the form  $F(C) \sim C^{1-\tau_C}$  at large  $C$ , with a similar agreement between the exponents of the intra- and interspecific data sets:  $\tau_C = 1.53 \pm 0.02$  and  $1.53 \pm 0.02$ , respectively (Figure 2B). The discrepancy observed between the two data sets at the tail of the distributions can be explained by the different sizes of

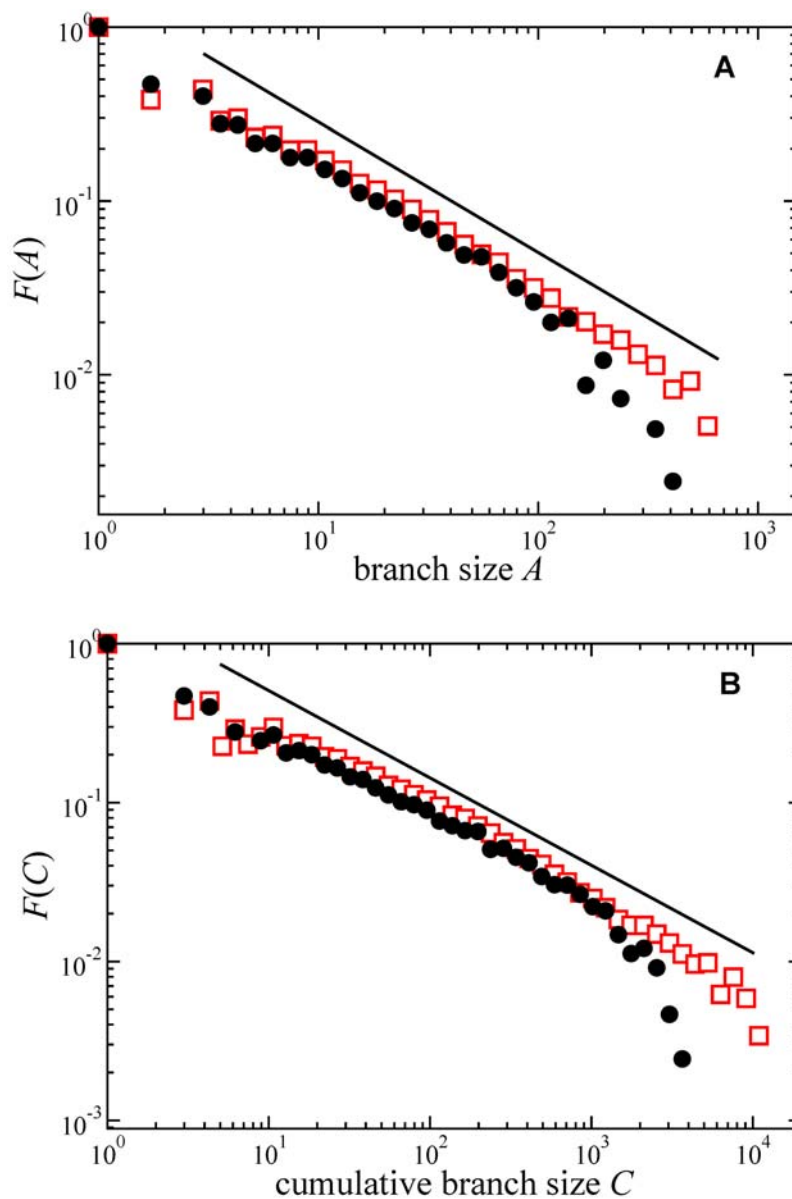
the typical trees on them: each tree contributes a natural cutoff to the overall distribution, and since the intraspecific trees are smaller in average, their cutoff appears at smaller tree sizes.

The allometric exponent,  $\eta$ , that characterizes the scaling of tree shape with tree size (Figure 3A), is also remarkably similar for the intraspecific ( $\eta = 1.43 \pm 0.01$ ) and the interspecific ( $\eta = 1.44 \pm 0.01$ ) phylogenies. This constancy of the exponents is still more remarkable when realizing (inset of Figure 3A) that it does not only apply to average properties of sets of intraspecific and interspecific trees, but also to individual phylogenies of groups of organisms pertaining to different kingdoms and living across widely contrasting environments, as it is reflected by the very narrow range of  $\eta$  obtained from different phylogenies ( $\langle \eta \rangle = 1.47$ ,  $\sigma = 0.03$ , Figure 3A). The scaling exponents for our large interspecific data set are also matched almost perfectly (Figure S1) by those derived from a set of 67 interspecific phylogenies randomly drawn from the published literature thereby validating the uniformity of the scaling rules of the broad interspecific phylogenies and the smaller set of intraspecific ones used here. The later was also derived from a similar random sample taken from the published literature (see Text S1).

The allometric scaling of  $C \sim A^{1.44}$  derived from our analysis falls somehow in between those obtained by simulated phylogenies derived from two extreme topologies: The symmetric tree gives  $C \sim A \ln A$ , which corresponds to  $\eta = 1$  with a logarithmic correction, while the pectinate tree has  $\eta = 2$ . The natural null model for tree construction, the Equal-Rates Markov (ERM) model [14,15], yields a scaling  $C \sim A \ln A$  similar to the symmetric tree with  $\eta = 1$  but different from the scaling displayed by empirical inter- and intraspecific phylogenies, particularly for large ones (Figure 3B). Therefore some topological aspects of phylogenetic trees are not adequately reproduced by the ERM model. Our results imply that successful lineages diversify more profusely than expected under random branching, generating the large imbalances that characterize emerging depictions of the Tree of Life [4]. Alternative models introducing correlations, such as the proportional-to-distinguishable-arrangements (PDA) model [4,16] or the beta splitting model [17], could generate more realistic phylogenies. Guided by previous biological allometric scaling analysis, we have assumed a power-law scaling of the form  $C \sim A^\eta$ . However, other ansatz could also fit the data. The important point, however, is that these modeling approaches should give similar scaling properties for intra- as for interspecific branching.

## Discussion

Traditionally, microevolutionary and macroevolutionary processes have been studied independently by population geneticists and evolutionary biologists, respectively [18]. The divide between these two levels of generation of biological diversity is an old one, rooted in the controversy between Darwinian gradualism and the saltationism proposed by others, prominently paleontologists, to explain macroevolutionary processes [19]. The debate as to whether macroevolution is more than the accumulation of microevolutionary events remains active [18,20,21], although refined paleontological evidence supports the continuum between micro- and macroevolution for some lineages [22]. The results presented here show that the branching and scaling patterns in intraspecific and interspecific phylogenies do not differ significantly for the topological properties we have calculated. Thus, shall saltation processes be a factor at the macroevolutionary level, this is not reflected in the topology of phylogenetic branching as examined here. Evidence for possible differences in phylogenetic topologies between the inter- and intraspecific levels may require a detailed analysis of branching times, which we have not attempted.

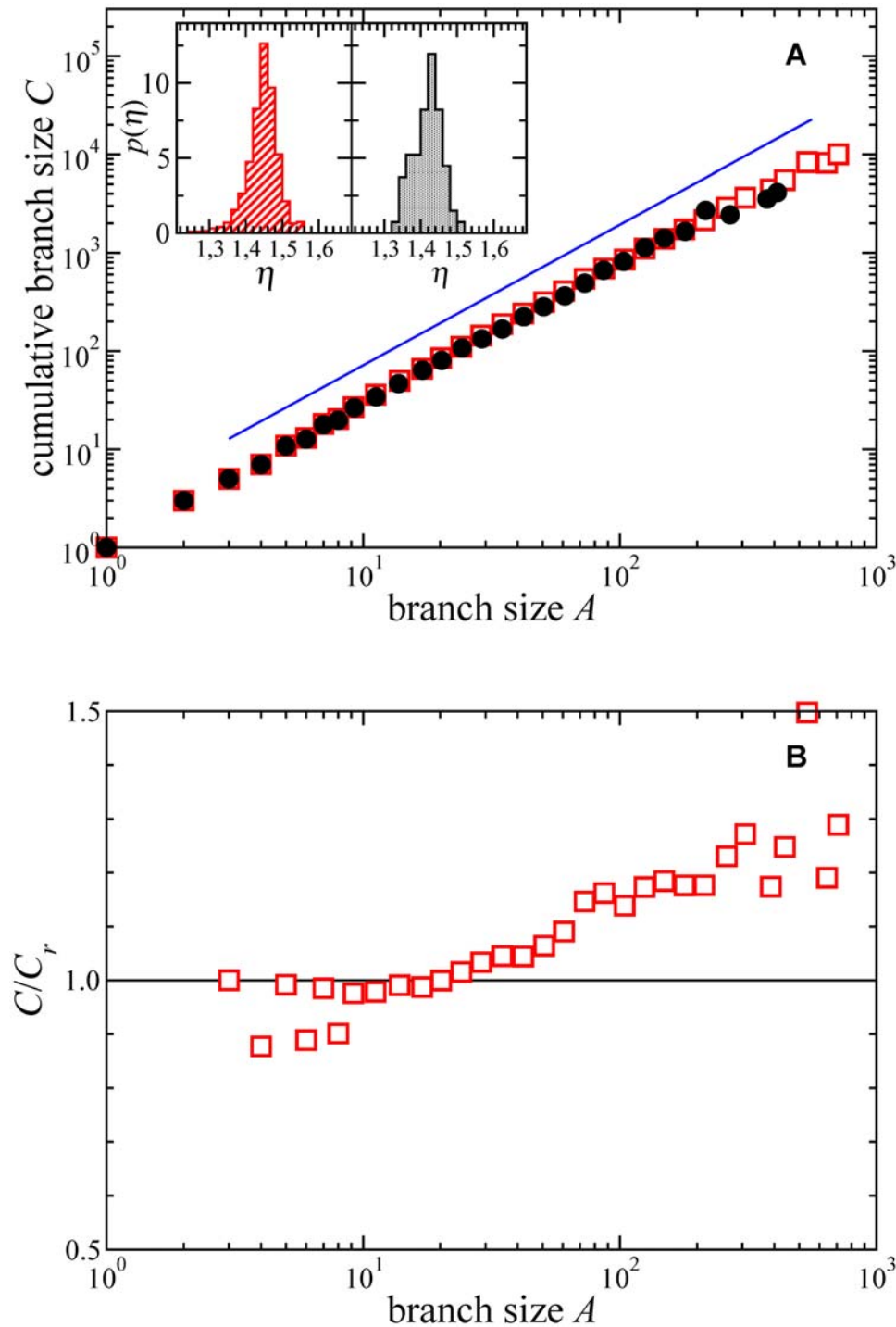


**Figure 2. Average distributions.** Cumulative complementary distribution functions (CCDFs) averaged and logarithmically binned over all phylogenetic trees in the interspecific (empty squares) and intraspecific (solid circles) data sets. A: CCDF of branch size,  $F(A)$ . Solid line corresponds to a power law  $F(A) \sim A^{1-\tau_A}$  with the exponent given by the best fit to the interspecific data set  $\tau_A = 1.74$ . B: CCDF of the cumulative branch size,  $F(C)$ . The line corresponds to a power law with the exponent given by the best fit to the interspecific data set  $\tau_C = 1.53$ . doi:10.1371/journal.pone.0002757.g002

Processes leading to scaling laws in size distributions in natural systems have been formulated as growth models [23,24]. Many of the findings carry over to scaling properties found in networks [25] and their description in terms of branching processes [26]. But most of these models predict branching topologies similar to the ERM model. An alternative approach to understand the observed exponent would be to trace analogies with scaling laws in different branching systems [5,6,27] which have been explained by invoking a natural optimization criterion based in the fact that the observed trees contain the largest possible number of apices within the smallest number of branching levels. For binary trees of size  $A$ , where nodes are restricted to occupy uniformly a  $D$  dimensional Euclidean space, the minimum value of  $C$  scales as  $A^\eta$ , with  $\eta = (D+1)/D$ . This scaling also describes the  $D$ -dimensional tree with the maximum size for a given depth (the average distance

between root and leaves). The value of  $\eta$  obtained in our phylogeny analysis,  $\eta \cong 1.44$ , is achieved only for optimal trees restricted to spaces of  $D \cong 2.27$  dimensions. Given the apparently unlimited number of variables that may yield differences among taxa, restricting their representation to a space with such a small number of dimensions seems unreasonable. This interpretation suggests that the evolutionary process yielding the observed phylogenies is not the most parsimonious one, which could potentially yield a similar biodiversity with fewer branching levels. In fact, the natural choice  $D = \infty$  gives an optimal exponent  $\eta = 1$ , which correspond to the ERM value and departs from observed scaling. Optimal traffic networks [28] also led to the exponent  $\tau_A = 2$  which departs from the empirical scaling exponent reported here for phylogenetic trees.

In summary, the remarkably similar allometric exponents reported here to characterize universally the scaling properties of



**Figure 3. Allometric scaling.** A: Plot of the logarithmically binned set of values of branch size,  $A$ , and cumulative branch size,  $C$ , for the interspecific (empty squares) and intraspecific (solid circles) data sets considered. The line corresponds to a power law  $C \sim A^\eta$ , with the exponent given by the best fit through all data,  $\eta = 1.44$ . The inset shows probability distributions of the values of  $\eta$  fitted to each individual tree (left: interspecific, right: intraspecific data sets) illustrating the small dispersion in the values. B: Plot of the logarithmically binned set of values of  $C$  as a function of  $A$  for the interspecific data, normalized by the prediction from the ERM model (the horizontal line). Data systematically deviate from ERM, especially for large size  $A$ .

doi:10.1371/journal.pone.0002757.g003

intra- and inter-specific phylogenies across kingdoms, reproductive systems and environments, strongly suggests the conservation of branching rules, and hence of the evolutionary processes that drive biological diversification, across the entire history of life. Although at short branch sizes the topology of observed phylogenies cannot

differ much from that expected under random and symmetric trees, due to the restriction of binary bifurcations in phylogenetic tree reconstruction, significant departures become universally evident as trees become larger, where the null ERM model and real phylogenies differ (Figure 2B). These deviations suggest (a)

that the evolution of life leads to less biodiversity than an optimal tree can possibly generate; and (b) the operation of a mechanism generating a correlated branching, where some memory of past evolutionary events is maintained along each branch. This correlated branching pattern implies that entities that diversify faster than average lead to new biological forms that diversify more than average themselves. Invariance across the broad scales considered here indicates that relatively simple rules govern the phylogenetic branching and the unfolding of biodiversity. Their deviation from random models indicates that evolutionary success is a correlated trait within lineages, yielding present asymmetries in the structure of the Tree of Life.

## Materials and Methods

### Phylogenies databases

On June 30th 2007 we downloaded the 5,212 phylogenetic trees available at that time in the database TreeBASE (<http://www.treebase.org>). TreeBASE constitutes a large database of interspecific phylogenies, which were collected from previously published research papers. The size of trees oscillates from 10 to 600 tips. Most of the bifurcations in these trees are binary, as confirmed by the fact that the ratio between the number of tips and the total number of nodes gives 0.52 when averaged over all the trees (for perfect binary trees, the ratio is 0.50).

As a comprehensive database comparable to TreeBASE does not exist for intraspecific phylogenies, we constructed an intraspecific data set by manually compiling 67 intraspecific phylogenies from several published phylogenetic analysis [S1–S45]. We compiled this data set in such a way that it contains: 1) Organisms from the main different environments (terrestrial, marine and fresh water), climatic regions (from polar to desert), and branches of life (Table S1). 2) Phylogenetic trees reconstructed with the main phylogenetic tree estimation methods, i.e., neighbor-joining, maximum parsimony and maximum likelihood methods.

In order to test whether the results derived from the examination of the relatively small (67 phylogenies) intraspecific data base can be compared with the much larger (5212) set of interspecific phylogenies extracted from TreeBASE, we sampled the literature to construct a dataset of 67 interspecific phylogenies drawn from the literature [S46–S85] using the same criteria as those to derived the intraspecific phylogeny data base (Table S1), obtaining full agreement (Figure S1). The intra- and interspecific phylogenies derived from the literature ranged between 30 and 170 tips, and they contained mainly binary branching events. An example for each kind of phylogenies is shown in Figures S2A and S3A.

### Branch size and cumulative branch size distributions

We associate to each node  $i$  of a phylogenetic tree two quantities, the size  $A_i$  (number of nodes) of the subtree  $S_i$  made up of node  $i$  and all the descendant nodes below it, that is, the subtree which does not contain the global root of the original tree, and the cumulative branch size,  $C_i$ , defined as the sum of the branch sizes associated to all the nodes in the subtree  $S_i$ ,  $C_i = \sum A_j$ . To characterize the probability distributions of the  $A_i$  and  $C_i$  values on a particular phylogenetic tree we compute the respective complementary cumulative distribution functions (CCDF):  $F(A) = \text{probability}(A_i > A)$ , and  $F(C) = \text{probability}(C_i > C)$ . We observe that these quantities scale, for large values of  $A$  and  $C$ , as power laws:  $F(A) \sim A^{1-\tau_A}$  and  $F(C) \sim C^{1-\tau_C}$ . The exponents  $\tau_A$  and  $\tau_C$ , thus, characterize the probabilities of  $\{A_i\}$  and  $\{C_i\}$ :  $P(A) \sim A^{-\tau_A}$  and  $P(C) \sim C^{-\tau_C}$ , respectively.

### Allometric scaling relationship

We observe that a functional relationship among the values of  $C$  and  $A$ , i.e. among shape and size, exists and also follows a power law,  $C \sim A^\eta$ , characterized by an exponent  $\eta$ . Since this relationship encodes the variation of a system property as size is varied, we can call this an *allometric scaling relationship*, to stress its connections with other functional relationships relating function and size [11,13,27]. We note that introduction of the change of variables  $C \sim A^\eta$  into  $F(C) \sim C^{1-\tau_C}$  leads to  $F(C) \sim A^{\eta(1-\tau_C)}$ , from which  $\eta = (1-\tau_A)/(1-\tau_C)$ . Thus, only two out of the three exponents are independent. As simple examples for which the above exponents can be computed by direct counting, we mention the pectinate or fully unbalanced tree, i.e. a tree in which all branching occurs successively along a single branch, characterized by the exponents  $\tau_A = 0$ ,  $\tau_C = 1/2$ ,  $\eta = 2$ , or the fully symmetric or Cayley tree, characterized by  $\tau_A = 2$ , and  $C \sim A \ln A$ , which except for the weak logarithmic correction corresponds to  $\eta = 1$  and  $\tau_C = 2$ . Figures S2B and S3B show, in contrast, the allometric scaling relationship for the particular examples of intra- and inter-specific phylogenies displayed in Figures S2A and S3A.

In order to investigate whether observations differ from random expectations, we have compared the allometric scaling found here with the prediction of a null model [29], the Equal-rates Markov (ERM) model. The ERM model was attributed to Harding [30], and to Cavalli-Sforza and Edwards [31], although it is based on models of the diversification process that date back at least to Yule [23]. The main assumption of the ERM model is that the phylogeny is the product of random branching. This is the result when the “effective speciation rate” (the difference between extinction and speciation rate) is equal for all species. The effective speciation rate may change chronologically, provided that it is the same for all lineages at a given time [23]. For this model we obtain  $C \sim A \ln A$ , or  $\eta = 1$ , and also  $\tau_A = \tau_C = 2$ . The random asymmetries introduced by the ERM are not strong enough to change the scaling behavior from the symmetric tree result.

The quantity  $C_i/A_i$  can be thought as a measure of the average *depth* or *distance* of the phylogenetic tree leaves to the node  $i$ . This can be seen taking into account that  $C_i = \sum (d_{ij} + 1)$ , where  $d_{ij}$  corresponds to the distance of each of the nodes  $j$  of the subtree  $S_i$  to the root  $i$ . Thus, the relationship between  $C$  and  $A$  can be written as  $C_i = A_i + \langle d \rangle_i A_i$ , where  $\langle d \rangle_i$  is the average depth of the nodes in the subtree  $S_i$ . The relationship between  $C_i/A_i$  and the depth is obtained:  $C_i/A_i = \langle d \rangle_i + 1$ . This quantity is closely related to the Sackin’s index defined as the distance of the leaves to the root:  $S = \sum_{i \in \text{leaves}} d_{i, \text{root}}$  [32,33]. It can be shown that for binary trees  $C = 2S + I$ , where  $C = \sum_{i \in \text{nodes}} d_{i, \text{root}}$ . Since the scaling law relating the increase of the depth or Sackin’s index with three size is known to be the same as the scaling of the Colless’ index, measuring the symmetry or balance of a phylogenetic tree [34], our results for  $\eta$  can be put in the context of the numerous studies available on the unbalance of phylogenetic trees [4,17,35]. Thus, connections between several methodologies previously used to analyze the topology of trees, such as size distributions [10,23], unbalance and depth [4,8,32–35], and transport efficiency [7,13,27,28], are revealed within the framework presented here.

### Supporting Information

**Text S1** Scaling of branch size and cumulative branch size: TreeBASE vs. manually selected data sets. We provide the list of references corresponding to the selected intraspecific and interspecific phylogenetic trees; the statistics of all data sets with two specific examples; and a summary table of taxa in the data sets.

Found at: doi:10.1371/journal.pone.0002757.s001 (0.06 MB DOC)

**Table S1** Break-down of the number of analyzed inter- and intra-species trees with respect to taxa.

Found at: doi:10.1371/journal.pone.0002757.s002 (0.03 MB DOC)

**Figure S1** Cumulative complementary distribution functions (CCDFs) for branch size ( $F(A)$ , panel A) and cumulative branch size ( $F(C)$ , panel B), and the allometric scaling relation ( $C$  {similar, tilde operator}  $A^n$ , panel B) averaged and logarithmically binned over all phylogenetic trees. Empty squares are for the interspecific TreeBASE data set, solid circles are for the manually compiled intraspecific data set, and triangles are for the new manually compiled interspecific data set of reduced size. Solid lines are power laws fitted to the TreeBASE behavior, as in Figs. 2 and 3 of the main text.

Found at: doi:10.1371/journal.pone.0002757.s003 (1.22 MB TIF)

**Figure S2** A: An example of an intraspecific phylogenetic tree: different strains of the bacteria *Vibrio vulnificus* [S19]. Most of the branchings are binary, but there are some 3rd order branchings.

## References

- Cracraft J, Donoghue MJ (2004) *Assembling the Tree of Life*. Oxford: Oxford University Press.
- Purvis S, Hector A (2000) Getting the measure of biodiversity. *Nature* 405: 212–219.
- Rokas A (2006) Genomics and the Tree of Life. *Science* 313: 1897–1899.
- Blum MGB, François O (2006) Which random processes describe the tree of life? A large-scale study of phylogenetic tree imbalance. *Syst Biol* 55: 685–691.
- Rodriguez-Iturbe I, Rinaldo A (1997) *Fractal river basins: chance and self-organization*. New York: Cambridge University Press.
- Makarieva AM, Gorshkov VG, Li B-L (2005) Revising the distributive networks models of West, Brown and Enquist (1997) and Banavar, Maritan and Rinaldo (1999): metabolic inequity of living tissues provides clues for the observed allometric scaling rules. *J Theor Biol* 237: 291–301.
- Garlaschelli D, Caldarelli G, Pietronero L (2003) Universal scaling relations in food webs. *Nature* 423: 165–168.
- Camacho J, Arenas A (2005) Food-web topology Universal scaling in food-web structure? *Nature* 435: E3–E4.
- Proulx SR, Promislow DEL, Phillips PC (2005) Network thinking in ecology and evolution. *Trends Ecol Evol* 20: 345–353.
- Klemm K, Eguiluz VM, San Miguel M (2005) Scaling in the structure of directory trees in a computer cluster. *Phys Rev Lett* 95: 128701.
- LaBarbera M (1989) Analyzing Body Size as a Factor in Ecology and Evolution. *Annu Rev Ecol Syst* 20: 97–117.
- Webb JK, Brook BW, Shine R (2002) What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecol Res* 17: 59–67.
- Banavar J, Maritan A, Rinaldo A (1999) Size and form in efficient transportation networks. *Nature* 399: 130–132.
- Mooers AO, Heard SB (1997) Inferring evolutionary process from phylogenetic tree shape. *Q Rev Biol* 72: 31–54.
- Caldarelli G, Cartozo CC, De Los Rios P, Servedio VDP (2004) Widespread occurrence of the inverse square distribution in social sciences and taxonomy. *Phys Rev E* 69: 035101(1–3).
- Pinelis I (2003) Evolutionary models of phylogenetic trees. *Proc R Soc Lond B* 270: 1425–1431.
- Aldous DJ (2001) Stochastic models and descriptive statistics for phylogenetic trees from Yule to today. *Stat Sci* 16: 23–34.
- Simons A (2002) The continuity of microevolution and macroevolution. *J Evol Biol* 15: 688–701.
- Mayr E (1982) Speciation and macroevolution. *Evolution* 36: 1119–1132.
- Grantham T (2007) Is macroevolution more than successive rounds of microevolution? *Palaeontology* 50: 75–85.
- Erwin DH (2000) Macroevolution is more than repeated rounds of microevolution. *Evol Dev* 2: 78–84.
- Kutschera U, Niklas KJ (2004) The modern theory of biological evolution: an expanded synthesis. *Naturwissenschaften* 91: 255–276.
- Yule GU (1924) A mathematical theory of evolution, based on the conclusions of Dr. J. C. Willis. *Philos Trans R Soc Lond A* 213: 21–87.
- Simon HA (1995) On a class of skew distribution functions. *Biometrika* 42: 425–440.
- Bornholdt S, Ebel H (2001) World Wide Web Scaling Exponent from Simon's 1955 Model. *Phys Rev E* 64: 035104(R).
- Durrett R (2007) *Random Graph Dynamics*. Cambridge: Cambridge University Press.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a Metabolic Theory of Ecology. *Ecology* 85: 1771–1789.
- Barthélemy M, Flammini A (2006) Optimal traffic networks. *J Stat Mech* 07: L07002.
- Harvey PH, Colwell RK, Silvertown JW, May RM (1983) Null models in ecology. *Ann Rev Ecol Syst* 14: 189–211.
- Harding EF (1971) The probabilities of rooted tree-shapes generated by random bifurcation. *Adv Appl Prob* 3: 44–77.
- Cavalli-Sforza LL, Edwards AWF (1967) Phylogenetic analysis: models and estimation procedures. *Evolution* 21: 550–570.
- Sackin MJ (1972) “Good” and “bad” phenograms. *Sys Zool* 21: 225–226.
- Shao KT, Sokal R (1990) Tree balance. *Sys Zool* 39: 226–276.
- Ford DJ (2006) Probabilities on cladograms: introduction to the alpha model (PhD Thesis, Stanford University).
- Holman EW (2005) Nodes in phylogenetic trees: the relation between imbalance and number of descendent species. *Syst Biol* 54: 895–899.

## SUPPORTING INFORMATION

### *Scaling of branch size and cumulative branch size: TreeBASE vs. manually selected data sets*

The interspecific data set analyzed in this paper consists of 5212 phylogenetic trees downloaded from TreeBASE (<http://www.treebase.org>). Given that a database similar to TreeBASE does not exist for intraspecific phylogenies, we constructed our intraspecific data set by manually compiling 67 phylogenetic trees from several published references [S1-S45]. The difference in size between the two data sets calls for some additional checking on the appropriateness of a comparison between them. As a way to close the gap between the two datasets we compiled a third set of trees consisting of phylogenies of interspecific character, like the data in TreeBASE, but manually extracted from published references [S46-85] following the same criteria as the intraspecific set analyzed in the paper, and with the same size, 67 trees. We remind (see main text) that our selection criteria insure that our tree datasets contained organisms from terrestrial, marine and fresh water environments, from all the main climatic regions, from all kingdoms (Table S1), and reconstructed with the main phylogenetic tree estimation methods.

The results of this analysis are shown in Figure S1 (we illustrate tree structures and the allometric scaling for one intraspecific and one interspecific tree in Figures S2 and S3, respectively). It displays the cumulative complementary distribution functions (CCDFs) for branch size ( $F(A)$ , panel a) and cumulative branch size ( $F(C)$ , panel b), and the allometric scaling relation ( $C \sim A^\eta$ , panel c) averaged and logarithmically binned over all phylogenetic trees. We see that, despite their different size, the two interspecific data sets display the same behavior. Any bias in the manual selection procedure with respect to

TreeBASE, if present, is weak enough to have no impact on the topological scaling behavior. In addition, there is perfect agreement between the scaling of the three data sets, except for the largest tree sizes for which there is poor statistics in the smaller data sets. This gives further support to the universality of the scaling found.



**Table S1. Break-down of the number of analyzed inter- and intra-species trees with respect to taxa.**

**Figure S1. Scaling relations from the enlarged data set described in Supporting Information.** Cumulative complementary distribution functions (CCDFs) for branch size ( $F(A)$ , panel A) and cumulative branch size ( $F(C)$ , panel B), and the allometric scaling relation ( $C \sim A^n$ , panel C) averaged and logarithmically binned over all phylogenetic trees. Empty squares are for the interspecific TreeBASE data set, solid circles are for the manually compiled intraspecific data set, and triangles are for the new manually compiled interspecific data set of reduced size. Solid lines are power laws fitted to the TreeBASE behavior, as in Figs. 2 and 3 of the main text.

**Figure S2. Intraspecific phylogenetic tree.** A: An example of an intraspecific phylogenetic tree: different strains of the bacteria *Vibrio vulnificus* [S19]. Most of the branchings are binary, but there are some 3rd order branchings. B: The allometric scaling plot showing the relationship of cumulative branch size ( $C$ ) to branch size ( $A$ ) from each node of that tree. The solid line corresponds to the fitting  $C \sim A^{1.43}$  to this intraspecific dataset.

**Figure S3. Interspecific phylogenetic tree.** A: An example of an interspecific phylogenetic tree: the catfish species (order *Siluriformes*) [S80]. Most of the branchings are binary, but there are some 3rd order branchings. B: The allometric scaling plot showing the

relationship of cumulative branch size ( $C$ ) to branch size ( $A$ ) from each node of that tree.

The solid line corresponds to the fitting  $C \sim A^{1.44}$  to this intraspecific dataset.

	INTER	INTRA
<i>Animalia</i>	26	24
<i>Archaea</i>	3	0
<i>Bacteria</i>	9	18
<i>Fungi</i>	13	6
<i>Plantae</i>	8	6
<i>Protozoa</i>	6	4
<i>Viruses</i>	2	9

**Table S1. Break-down of the number of analyzed inter- and intra-species trees with respect to taxa.**

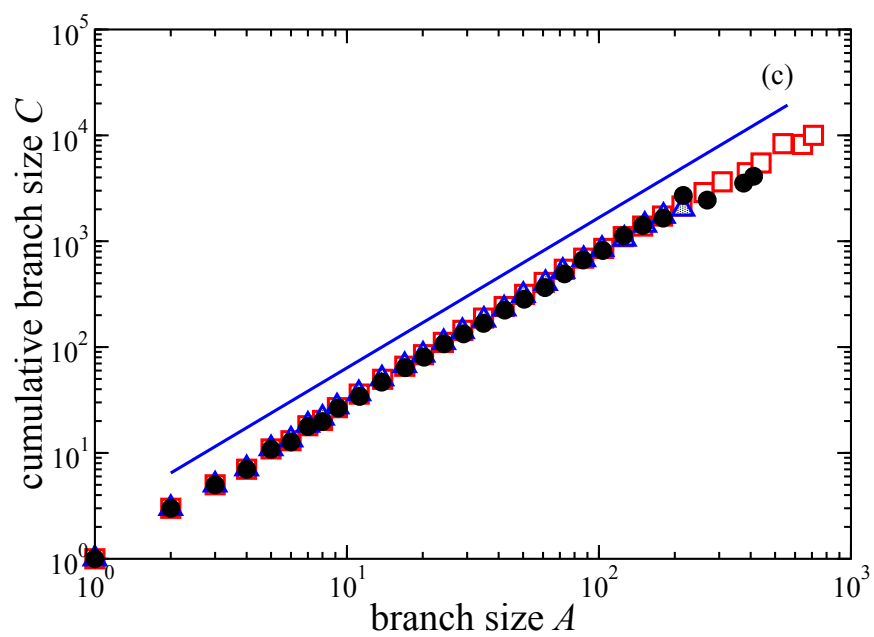
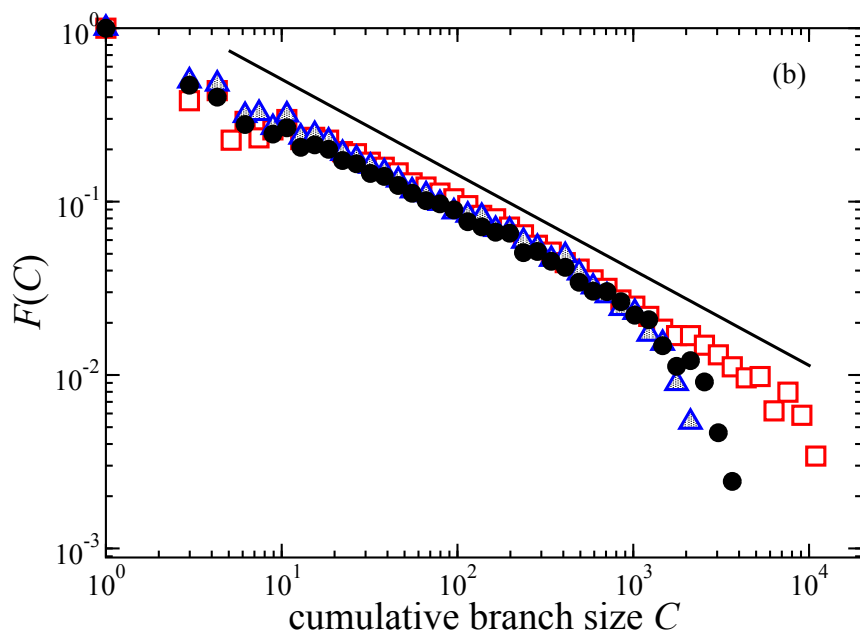
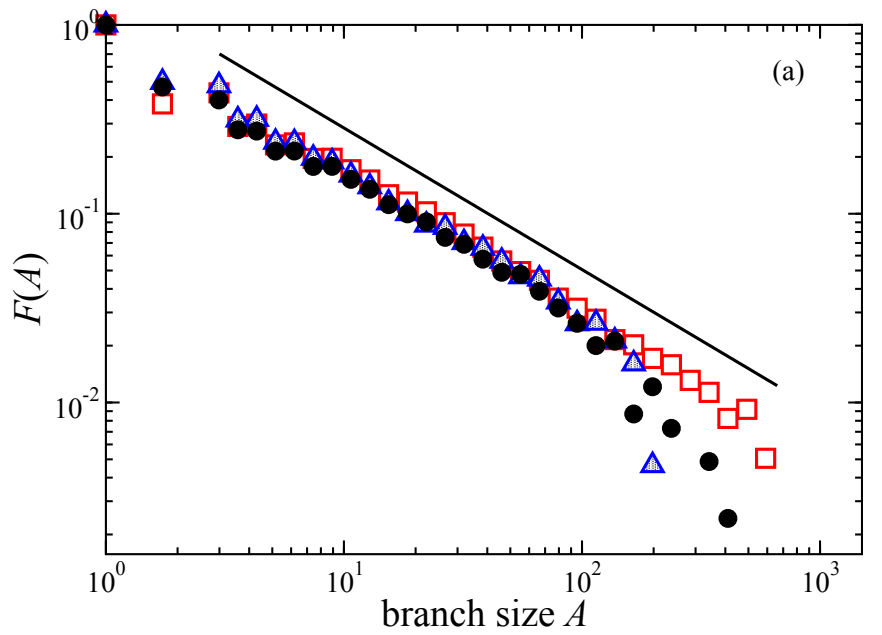


FIGURE S1

(a)

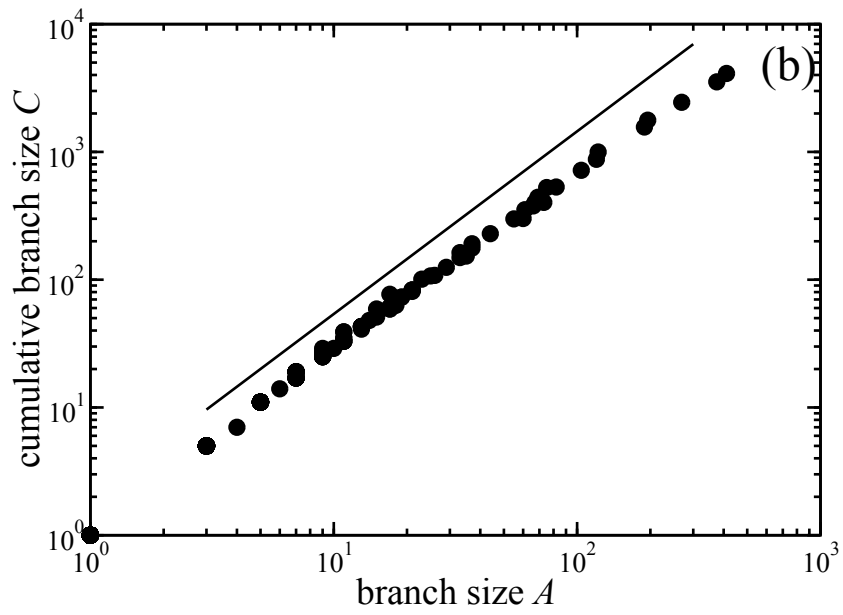
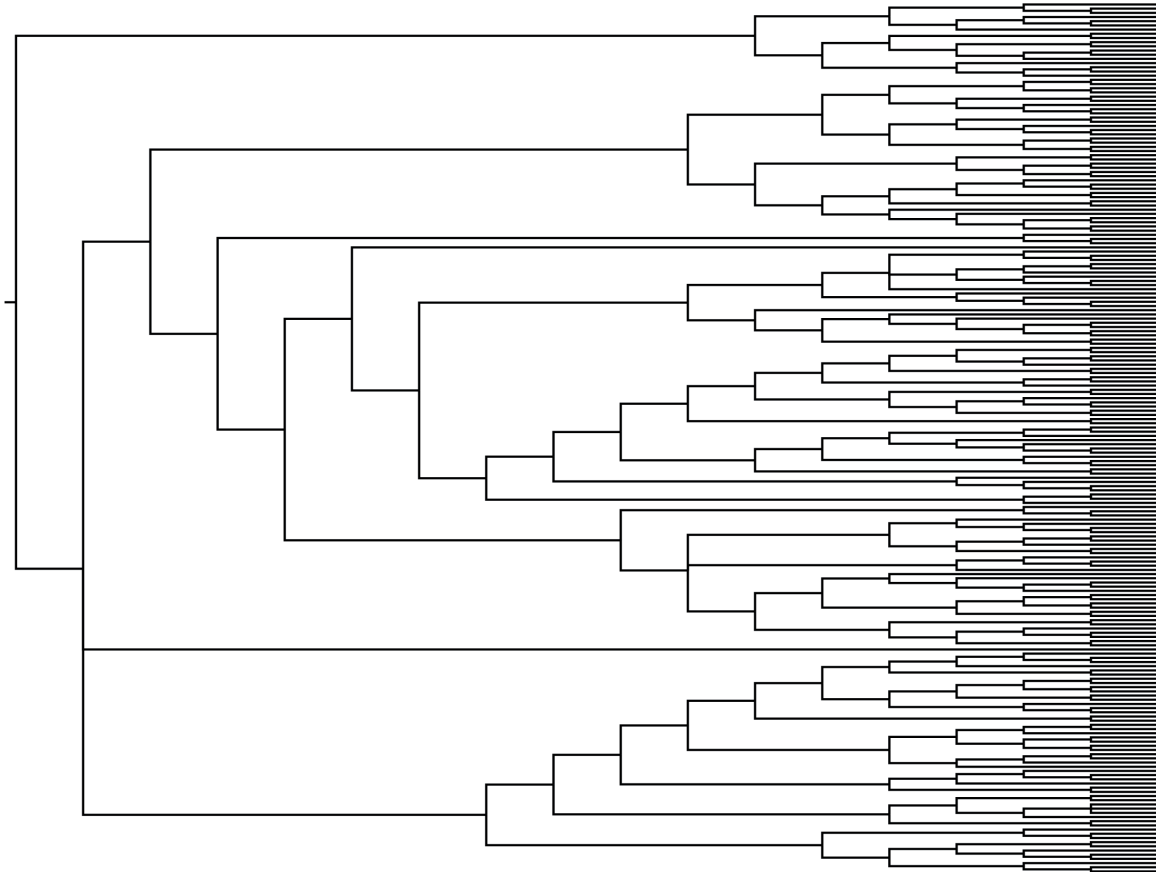


FIGURE S2

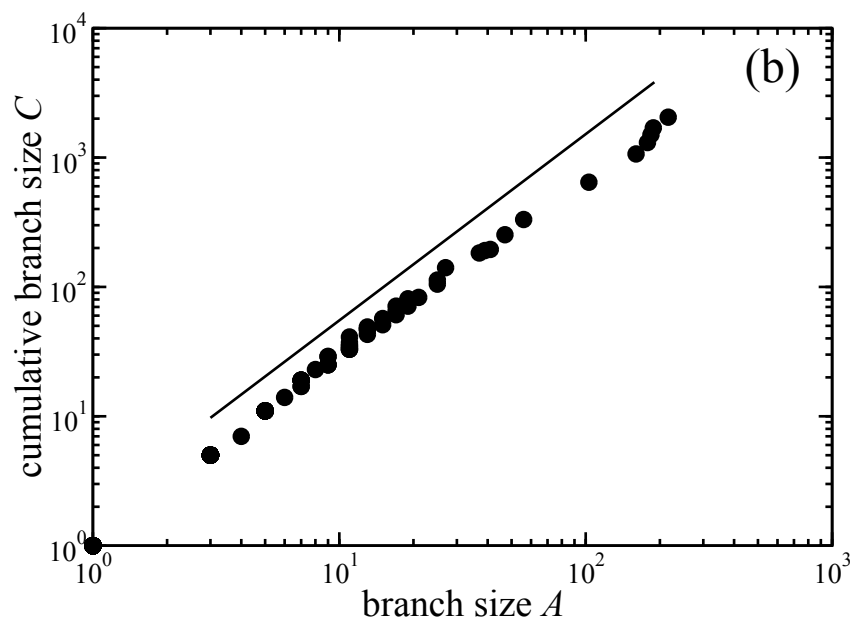
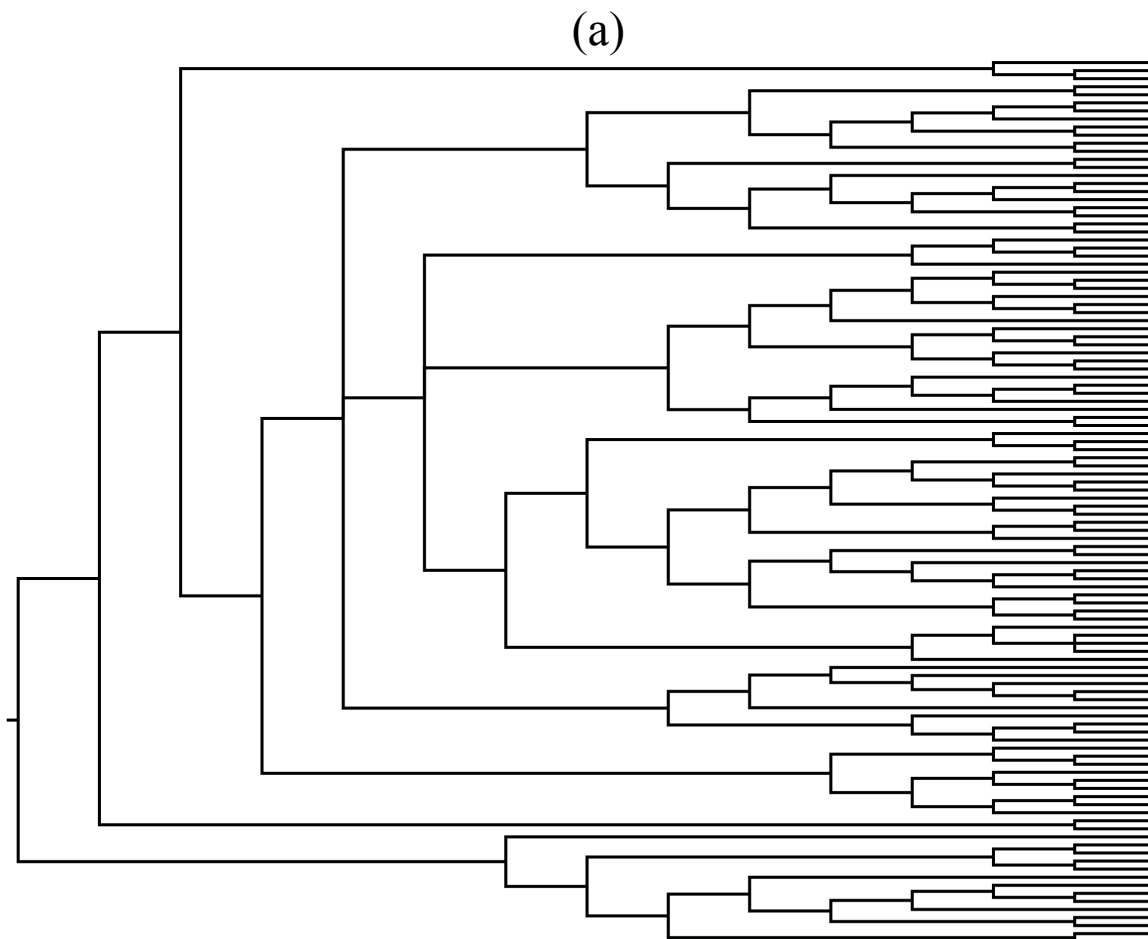


FIGURE S3

### **Intraspecific and interspecific data sets**

The intraspecific and interspecific phylogenies which have been analyzed, in addition to the ones from TreeBase, have been obtained from the following references:

#### ***Intraspecific phylogenies***

- S1. Albach DC, Schönswetter P, Tribsch A (2006) Comparative phylogeography of the *Veronica alpina* complex in Europe and North America. *Mol. Ecol.* 15: 3269-3286.
- S2. Beszteri B, Ács E, Medlin, LK (2005) Ribosomal DNA Sequence Variation among Sympatric Strains of the *Cyclotella meneghiniana* Complex (Bacillariophyceae) Reveals Cryptic Diversity. *Protist* 156: 317-333.
- S3. Choi Y-J, Hong S-B, Shin H-D (2006) Genetic diversity within the *Albugo candida* complex (Peronosporales, Oomycota) inferred from phylogenetic analysis of ITS rDNA and COX2 mtDNA sequences. *Mol. Phylogenet. Evol.* 40: 400-409.
- S4. Cupolillo E, Brahim LR, Toaldo CB, de Oliveira-Neto MP, de Brito MEF, Falqueto A, Naiff MdeF, Grimaldi GJr (2003) Genetic Polymorphism and Molecular Epidemiology of *Leishmania* (*Viannia*) *braziliensis* from Different Hosts and Geographic Areas in Brazil. *J. Clin. Microbiol.* 41: 3126-3132.
- S5. de Casas RR, Besnard G, Schönswetter P, Balaguer L, Vargas P (2006) Extensive gene flow blurs phylogeographic but not phylogenetic signal in *Olea europaea* L. *Theor. Appl. Genet.* 113: 575-583.
- S6. Devitt TJ (2006) Phylogeography of the Western Lyresnake (*Trimorphodon biscutatus*): testing aridland biogeographical hypotheses across the Nearctic-Neotropical transition. *Mol. Ecol.* 15: 4387-4407.
- S7. Driscoll DA, Hardy CM (2005) Dispersal and phylogeography of the agamid lizard *Amphibolurus nobbi* in fragmented and continuous habitat. *Mol. Ecol.* 14: 1613-1629.

- S8. Ehling-Schulz M, Svensson B, Guinebretiere M-H, Lindbäck T, Andersson M, Schulz A, Fricker M, Christiansson A, Granum PE, Märtlbauer E, Nguyen-The C, Salkinoja-Salonen M, Scherer S (2005) Emetic toxin formation of *Bacillus cereus* is restricted to a single evolutionary lineage of closely related strains. *Microbiology* 151: 183–197.
- S9. Gottschling M, Köhler A, Stockfleth E, Nindl I (2007) Phylogenetic analysis of beta-papillomaviruses as inferred from nucleotide and amino acid sequence data. *Mol. Phylogenet. Evol.* 42: 213–222.
- S10. Hahn MW, Pöckl M, Wu QL (2005) Low Intraspecific Diversity in a Polynucleobacter Subcluster Population Numerically Dominating Bacterioplankton of a Freshwater Pond. *Appl. Environ. Microbiol.* 71: 4539–4547.
- S11. Heilveil JS, Berlocher SH (2006) Phylogeography of postglacial range expansion in *Nigronia serricornis* Say (Megaloptera: Corydalidae). *Mol. Ecol.* 15: 1627–1641.
- S12. Hommais F, Pereira S, Acquaviva C, Escobar-Páramo P, Denamur E (2005) Single-Nucleotide Polymorphism Phylotyping of *Escherichia coli*. *Appl. Environ. Microbiol.* 71: 4784–4792.
- S13. Huang S, Chiang YC, Schaal BA, Chou CH, Chiang TY (2001) Organelle DNA phylogeography of *Cycas taitungensis*, a relict species in Taiwan. *Mol. Ecol.* 10: 2669–2681.
- S14. Humbert JF, Duris-Latour D, Le Berre B, Giraudet H, Salençon MJ (2005) Genetic Diversity in *Microcystis* Populations of a French Storage Reservoir Assessed by Sequencing of the 16S-23S rRNA Intergenic Spacer. *Microb. Ecol.* 49: 308–314.
- S15. Jensen LH, Enghoff H, Frydenberg J, Parker EDJr (2002) Genetic diversity and the phylogeography of parthenogenesis: comparing bisexual and thelytokous populations of *Nemasoma aricorne* (Diplopoda: Nemasomatidae) in Denmark. *Hereditas* 136: 184–194.



- S16. Kawamoto Y, Shotake T, Nozawa K, Kawamoto S, Tomari K-I, Kawai S, Shirai K, Morimitsu Y, Takagi N, Akaza H, Fujii H, Hagihara K, Aizawa K, Akachi S, Oi T, Hayaishi S (2007) Postglacial population expansion of Japanese macaques (*Macaca fuscata*) inferred from mitochondrial DNA phylogeography. *Primates* 48: 27-40.
- S17. Ko KS, Lee HK, Park MY, Kook YH (2003) Mosaic Structure of Pathogenicity Islands in *Legionella pneumophila*. *J. Mol. Evol.* 57: 63-72.
- S18. Lefébure T, Douady CJ, Gouy M, Trontelj P, Briolay J, Gibert J (2006) Phylogeography of a subterranean amphipod reveals cryptic diversity and dynamic evolution in extreme environments. *Mol. Ecol.* 15: 1797-1806.
- S19. Lin M, Payne DA, Schwarz JR (2003) Intraspecific Diversity of *Vibrio vulnificus* in Galveston Bay Water and Oysters as Determined by Randomly Amplified Polymorphic DNA PCR. *Appl. Environ. Microbiol.* 69: 3170-3175.
- S20. Liu J-X, Gao T-X, Zhuang Z-M, Jin X-S, Yokogawa K, Zhang Y-P (2006) Late Pleistocene divergence and subsequent population expansion of two closely related fish species, Japanese anchovy (*Engraulis japonicus*) and Australian anchovy (*Engraulis australis*). *Mol. Phylogenet. Evol.* 40: 712-723.
- S21. Marmi J, López-Giráldez F, MacDonald DW, Calafell F, Zholnerovskaya E, Domingo-Roura X (2006) Mitochondrial DNA reveals a strong phylogeographic structure in the badger across Eurasia. *Mol. Ecol.* 15: 1007-1020.
- S22. Marimon R, Gené J, Cano J, Trilles L, Lazéra MS, Guarro J (2006) Molecular Phylogeny of *Sporothrix schenckii*. *J. Clin. Microbiol.* 44: 3251-3256.
- S23. Martínez-Solano I, Teixeira J, Buckley D, García-París M (2006) Mitochondrial DNA phylogeography of *Lissotriton boscai* (Caudata, Salamandridae): evidence for old, multiple refugia in an Iberian endemic. *Mol. Ecol.* 15: 3375-3388.

- S24. Michitaka K, Tanaka Y, Horiike N, Duong TN, Chen Y, Matsuura K, Hiasa Y, Mizokami M, Onji M (2006) Tracing the History of Hepatitis B Virus Genotype D in Western Japan. *J. Med. Virol.* 78: 44–52.
- S25. Miller CR, Waits LP, Joyce P (2006) Phylogeography and mitochondrial diversity of extirpated brown bear (*Ursus arctos*) populations in the contiguous United States and Mexico. *Mol. Ecol.* 15: 4477–4485.
- S26. Monis PT, Andrews RH, Mayrhofer G, Ey PL (2003) Genetic diversity within the morphological species *Giardia intestinalis* and its relationship to host origin. *Infect. Genet. Evol.* 3: 29–38.
- S27. Ozeki M, Isagi Y, Tsubota H, Jacklyn P, Bowman DMJS (2007) Phylogeography of an Australian termite, *Amitermes laurensis* (Isoptera, Termitidae), with special reference to the variety of mound shapes. *Mol. Phylogenet. Evol.* 42: 236–247.
- S28. Perneel M, Tambong JT, Adiobo A, Floren C, Saborío F, Lévesque A, Höfte M (2006) Intraspecific variability of *Pythium myriotylum* isolated from cocoyam and other host crops. *Mycol. Res.* 110: 583 – 593.
- S29. Perk S, Banet-Noach C, Shihmanter E, Pokamunski S, Pirak M, Lipkind M, Panshina A (2006) Genetic characterization of the H9N2 influenza viruses circulated in the poultry population in Israel. *Comp. Immunol. Microbiol. Infect. Dis.* 29: 207–223.
- S30. Roberts TE (2006) History, ocean channels, and distance determine phylogeographic patterns in three widespread Philippine fruit bats (Pteropodidae). *Mol. Ecol.* 15: 2183–2199.
- S31. Rowe KC, Heske EJ, Paige KN (2006) Comparative phylogeography of eastern chipmunks and white-footed mice in relation to the individualistic nature of species. *Mol. Ecol.* 15: 4003–4020.

- S32. Ruzzante DE, Walde SJ, Cussac VE, Dalebout ML, Seibert J, Ortubay S, Habit E (2006) Phylogeography of the Percichthyidae (Pisces) in Patagonia: roles of orogeny, glaciation, and volcanism. *Mol. Ecol.* 15: 2949–2968.
- S33. Scott JB, Chakraborty S (2006) Multilocus sequence analysis of *Fusarium pseudograminearum* reveals a single phylogenetic species. *Mycol. Res.* 110: 1413–1425.
- S34. Sogstad MKR, Høyby EA, Caugant DA (2006) Molecular Characterization of Non-Penicillin-Susceptible *Streptococcus pneumoniae* in Norway. *J. Clin. Microbiol.* 44: 3225–3230.
- S35. Thangadurai R, Hoti SL, Kumar NP, Das PK (2006) Phylogeography of human lymphatic filarial parasite, *Wuchereria bancrofti* in India. *Acta Trop.* 98: 297–304.
- S36. Ursenbacher S, Carlsson M, Helfer V, Tegelström H, Fumagalli L (2006) Phylogeography and Pleistocene refugia of the adder (*Vipera berus*) as inferred from mitochondrial DNA sequence data. *Mol. Ecol.* 15: 3425–3437.
- S37. Vancanneyt M, Huys G, Lefebvre K, Vankerckhoven V, Goossens H, Swings J (2006) Intraspecific Genotypic Characterization of *Lactobacillus rhamnosus* Strains Intended for Probiotic Use and Isolates of Human Origin. *Appl. Environ. Microbiol.* 72: 5376–5383.
- S38. van Ee BW, Jelinski N, Berry PE, Hipp AL (2006) Phylogeny and biogeography of *Croton alabamensis* (Euphorbiaceae), a rare shrub from Texas and Alabama, using DNA sequence and AFLP data. *Mol. Ecol.* 15: 2735–2751.
- S39. Verovnik R, Sket B, Trontelj P (2004) Phylogeography of subterranean and surface populations of water lice *Asellus aquaticus* (Crustacea: Isopoda). *Mol. Ecol.* 13: 1519–1532.

- S40. Ward TJ, Gorski L, Borucki MK, Mandrell RE, Hutchins J, Pupedis K (2004) Intraspecific Phylogeny and Lineage Group Identification Based on the *prfA* Virulence Gene Cluster of *Listeria monocytogenes*. *J. Bacteriol.* 186: 4994–5002.
- S41. Whipps CM, Kent ML (2006) Phylogeography of the Cosmopolitan Marine Parasite *Kudoa thyrsites* (Myxozoa: Myxosporia). *J. Eukaryot. Microbiol.* 53: 364–373.
- S42. Zhang C, Mammen MPJr, Chinnawirotpisan P, Klungthong C, Rodpradit P, Nisalak A, Vaughn DW, Nimmannitya S, Kalayanarooj S, Holmes EC (2006) Structure and age of genetic diversity of dengue virus type 2 in Thailand. *J. Gen. Virol.* 87: 873–883.
- S43. Zhang W-J, Yang J, Yu Y-H, Shu S-W, Shen Y-F (2006) Population Genetic Structure of *Carchesium polypinum* (Ciliophora: Peritrichia) in Four Chinese Lakes Inferred from ISSR Fingerprinting: High Diversity but Low Differentiation. *J. Eukaryot. Microbiol.* 53: 358–363.
- S44. Zink RM, Drovetski SV, Rohwer S (2006) Selective neutrality of mitochondrial ND2 sequences, phylogeography and species limits in *Sitta europaea*. *Mol. Phylogenet. Evol.* 40, 679–686.
- S45. Zorrilla I, Moriñigo MA, Castro D, Balebona MC, Borrego JJ (2003) Intraspecific characterization of *Vibrio alginolyticus* isolates recovered from cultured fish in Spain. *J. Appl. Microbiol.* 95: 1106–1116.

### ***Interspecific phylogenies***

- S46. Andreasen K, Bremer B (2000) Combined phylogenetic analysis in the rubiaceae-ixoroideae: morphology, nuclear and chloroplast DNA data. *Am. J. Bot.* 87: 1731–1748.

- S47. Benz B W, Robbins MB, Peterson A T (2006) Evolutionary history of woodpeckers and allies (Aves: Picidae): Placing key taxa on the phylogenetic tree. *Mol. Phylogenet. Evol.* 40: 389–399.
- S48. Brindefalk B, Viklund J, Larsson D, Thollesson M, Andersson SG (2007) Origin and Evolution of the Mitochondrial Aminoacyl-tRNA Synthetases. *Mol. Biol. Evol.* 24: 743-756.
- S49. Dighe AS, Jangid K, González JM, Pidiyar VJ, Patole, MS, Ranade DR, Shouche YS (2004) Comparison of 16S rRNA gene sequences of genus *Methanobrevibacter*. *BMC Microbio.* 4: 20.
- S50. Dohrmann M, Voigt O, Erpenbeck D, Wörheide G (2006) Non-monophyly of most supraspecific taxa of calcareous sponges (Porifera, Calcarea) revealed by increased taxon sampling and partitioned Bayesian analysis of ribosomal DNA. *Mol. Phylogenet. Evol.* 40: 830–843.
- Duda TF Jr, Kohn AJ (2005) Species-level phylogeography and evolutionary history of the hyperdiverse marine gastropod genus *Conus*. *Mol. Phylogenet. Evol.* 34: 257–272.
- S51. Ellison NW, Liston A, Steiner JJ, Williams WM, Taylor NL (2006) Molecular phylogenetics of the clover genus (*Trifolium*—Leguminosae). *Mol. Phylogenet. Evol.* 39: 688–705.
- S52. Endress PK, Doyle JA (2007) Floral phyllotaxis in basal angiosperms: development and evolution. *Curr. Opin. Plant Biol.* 10: 52-57.
- S53. Fitzpatrick DA, Logue ME, Stajich JE, Butler G (2006) A fungal phylogeny based on 42 complete genomes derived from supertree and combined gene analysis. *BMC Evol. Biol.* 6: 99.

- S54. Fuchs J, Cruaud C, Couloux A, Pasquet E (2007) Complex biogeographic history of the cuckoo-shrikes and allies (Passeriformes: Campephagidae) revealed by mitochondrial and nuclear sequence data. *Mol. Phylogenet. Evol.* 44: 138–153.
- S55. Fulton TL, Strobeck C (2006) Molecular phylogeny of the Arctoidea (Carnivora): Effect of missing data on supertree and supermatrix analyses of multiple gene data sets. *Mol. Phylogenet. Evol.* 41: 165–181.
- S56. Gamage DT, de Silva MP, Inomata N, Yamazaki T, Szmidt AE (2006) Comprehensive molecular phylogeny of the sub-family dipteroocarpoideae (dipteroocarpaceae) based on chloroplast DNA sequences. *Genes Genet. Syst.* 81: 1-12.
- S57. García D, Stchigel AM, Cano J, Caldusch M, Hawksworth DL, Guarro J (2006) Molecular phylogeny of Coniochaetales. *Mycol. Res.* 110: 1271–1289.
- S58. Garcia J-L, Patel BK, Ollivier B (2000) Taxonomic, Phylogenetic, and Ecological Diversity of Methanogenic Archaea. *Anaerobe* 6: 205-226.
- S59. Gast RJ (2006) Molecular Phylogeny of a Potentially Parasitic Dinoflagellate Isolated from the Solitary Radiolarian, *Thalassicolla nucleata*. *J. Eukaryot. Microbiol.* 53: 43–45.
- S60. Gaubert P, Cordeiro-Estrela P (2006) Phylogenetic systematics and tempo of evolution of the Viverrinae (Mammalia, Carnivora, Viverridae) within feliformians: Implications for faunal exchanges between Asia and Africa. *Mol. Phylogenet. Evol.* 41: 266–278.
- S61. Habaye MS, Ekengren SK, Hultmark D (2006) Nora virus, a persistent virus in *Drosophila*, defines a new picorna-like virus family. *J. Gen. Virol.* 87: 3045–3051.
- S62. Hahn WJ (2002) A Molecular Phylogenetic Study of the Palmae (Arecaceae) Based on *atpB*, *rbcL*, and 18S nrDNA Sequences. *Syst. Biol.* 51: 92–112.

- S63. Huang L-N, Zhu S, Zhou H, Qu L-H (2005) Molecular phylogenetic diversity of bacteria associated with the leachate of a closed municipal solid waste landfill. *FEMS Microbiol. Lett.* 242: 297–303.
- S64. Hyvönen J, Koskinen S, Merrill GL, Hedderson TA, Stenroos S (2004) Phylogeny of the Polytrichales (Bryophyta) based on simultaneous analysis of molecular and morphological data. *Mol. Phylogenet. Evol.* 31: 915–928.
- S65. Lavoué S, Miya M, Saitoh K, Ishiguro NB, Nishida M (2007) Phylogenetic relationships among anchovies, sardines, herrings and their relatives (Clupeiformes), inferred from whole mitogenome sequences. *Mol. Phylogenet. Evol.* 43: 1096–1105.
- S66. Le M, Raxworthy CJ, McCord WP, Mertz L (2006) A molecular phylogeny of tortoises (Testudines: Testudinidae) based on mitochondrial and nuclear genes. *Mol. Phylogenet. Evol.* 40: 517–531.
- S67. Li L, Song W, Warren A, Wang Y, Ma H, Hu X, Chen Z (2006) Phylogenetic position of the marine ciliate, *Cardiostomatella vermiforme* (Kahl, 1928) Corliss, 1960 inferred from the complete SSrRNA gene sequence, with establishment of a new order *Loxocephalida* n. ord. (Ciliophora, Oligohymenophorea). *Eur. J. Protistol.* 42: 107–114.
- S68. Mallatt J, Giribet G (2006) Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. *Mol. Phylogenet. Evol.* 40: 772–794.
- S69. Mann NI, Barker FK, Graves JA, Dingess-Mann KA, Slater PJ (2006) Molecular data delineate four genera of “Thryothorus” wrens. *Mol. Phylogenet. Evol.* 40: 750–759.
- S70. Maraun M, Heethoff M, Schneider K, Scheu S, Weigmann G, Cianciolo J, Thomas RH, Norton RA (2004) Molecular phylogeny of oribatid mites (Oribatida, Acari):

- evidence for multiple radiations of parthenogenetic lineages. *Exp. Appl. Acarol.* 33: 183–201.
- S71. Moreira D, von der Heyden S, Bass D, López-García P, Chao E, Cavalier-Smith T (2007) Global eukaryote phylogeny: Combined small- and large-subunit ribosomal DNA trees support monophyly of Rhizaria, Retaria and Excavata. *Mol. Phylogenet. Evol.* 44: 255–266.
- S72. Moyle RG, Marks BD (2006) Phylogenetic relationships of the bulbuls (Aves: Pycnonotidae) based on mitochondrial and nuclear DNA sequence data. *Mol. Phylogenet. Evol.* 40: 687–695.
- S73. Ohlson JJ, Prum RO, Ericson PG (2007) A molecular phylogeny of the cotingas (Aves: Cotingidae). *Mol. Phylogenet. Evol.* 42: 25–37.
- S74. Robalo JJ, Almada VC, Levy A, Doadrio I (2007) Re-examination and phylogeny of the genus *Chondrostoma* based on mitochondrial and nuclear data and the definition of 5 new genera. *Mol. Phylogenet. Evol.* 42: 362–372.
- S75. Sagegami-Oba R, Oba Y, Ôhira H (2007) Phylogenetic relationships of click beetles (Coleoptera: Elateridae) inferred from 28S ribosomal DNA: Insights into the evolution of bioluminescence in Elateridae. *Mol. Phylogenet. Evol.* 42: 410–421.
- S76. Saldarriaga JF, McEwan ML, Fast NM, Taylor FJ, Keeling PJ (2003) Multiple protein phylogenies show that *Oxyrrhis marina* and *Perkinsus marinus* are early branches of the dinoflagellate lineage. *Int. J. Syst. Evol. Microbiol.* 53: 355–365.
- S77. Sjölin E, Erséus C, Källersjö M (2005) Phylogeny of Tubificidae (Annelida, Clitellata) based on mitochondrial and nuclear sequence data. *Mol. Phylogenet. Evol.* 35: 431–441.



- S78. Sørensen MV, Giribet G (2006) A modern approach to rotiferan phylogeny: Combining morphological and molecular data. *Mol. Phylogenet. Evol.* 40: 585–608.
- S79. Stchigel AM, Cano J, Miller AN, Caldusch M, Guarro J (2006) *Corylomyces*: a new genus of Sordariales from plant debris in France. *Mycol. Res.* 110: 1361–1368.
- S80. Sullivan JP, Lundberg JG, Hardman M (2006) A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using *rag1* and *rag2* nuclear gene sequences. *Mol. Phylogenet. Evol.* 41: 636–662.
- S81. Wang Z, Binder M, Schoch CL, Johnston PR, Spatafora JW, Hibbett DS (2006) Evolution of helotialean fungi (Leotiomycetes, Pezizomycotina): A nuclear rDNA phylogeny. *Mol. Phylogenet. Evol.* 41: 295–312.
- S82. Wright A-D (2006) Phylogenetic relationships within the order Halobacteriales inferred from 16S rRNA gene sequences. *Int. J. Syst. Evol. Microbiol.* 56: 1223–1227.
- S83. Zanatta DT, Murphy RW (2006) Evolution of active host-attraction strategies in the freshwater mussel tribe Lampsilini (Bivalvia: Unionidae). *Mol. Phylogenet. Evol.* 41: 195–208.
- S84. Zhang Z, Kudo T, Nakajima Y, Wang Y (2001) Clarification of the relationship between the members of the family Thermomonosporaceae on the basis of 16S rDNA, 16S–23S rRNA internal transcribed spacer and 23S rDNA sequences and chemotaxonomic analyses. *Int. J. Syst. Evol. Microbiol.* 51: 373–383.
- S85. Zuccon D, Cibois A, Pasquet E, Ericson PG (2006) Nuclear and mitochondrial sequence data reveal the major lineages of starlings, mynas and related taxa. *Mol. Phylogenet. Evol.* 41: 333–344.